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Why do animals have territories?

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Summary

In *chapter 2* an attempt is made to develop a scheme to classify the multitude of different and often mutually incompatible theoretical approaches that exist in the field. It is argued that the interaction between territory owners and intruders has to be seen as a bilateral conflict in the game-theoretical sense. It is then shown that the use of similar terminology by existing studies with very different approaches obscures the fact that there are three different types of territorial conflicts with different stakes and very different properties.

Assuming a non-territorial population represents the ancestral state, it is not very well understood how territorial behaviour could evolve in such a population. Previous studies have shown that if (presumably agonistic) interactions between individuals are costly in terms of fitness, then avoidance of neighbours or space that belongs to neighbours can spread in a population. *Chapter 3* investigates under which conditions individuals would start behaving agonistically, thereby causing high interaction costs, in a non-territorial population in the first place. It turns out that patchiness of resources, population density, asymmetries between contestants and number as well as sequence of decisions available to them interact in complex ways to determine the evolution of defence. Defence of homogeneously distributed resources evolves a.o. if losers in a contest can decide how far to run, if aggressiveness is based on a critical distance or if decisions are not simultaneous.

In *chapter 4* an existing simple, spatially explicit model is extended to enable a full evolutionary analysis of a contiguous strategy space. Contrary to the original results it is demonstrated that whether avoidance can spread and to which degree it actually leads to spatially separated territories depends very much on which kind of conflict strategies are possible in the population as well as on which ones are present initially.

Evolutionarily stable territoriality can only occur if the costs of defending a territory against intruders are lower than the fitness gained by having exclusive access to the resources inside it. Stealing from a territory on the other hand pays if the expected gain in resources exceeds the expected costs of being attacked by the owner. In *chapter 5* it is shown that in a scenario

with explicit resource dynamics it generally pays for territorial neighbours to steal from each other in order to minimize local resource depletion, even if territory owners forage with significantly higher efficiency. Only if fighting is very costly for intruders or if crossing territory borders does carry a fitness cost can defence against theft evolve.

This finding is counter-intuitive as well as at odds with the many observations of territorial populations in which there seem to be negligible levels of theft. *Chapter 6* demonstrates that deterrence can be an effective mechanism in stabilizing territoriality against theft. Assuming a generalized owner-floater scenario it is shown that if the owner's willingness to defend varies in the population while intruders are able to detect owner behaviour and react to it then the owners' aggressiveness and the intruders' cautiousness will reinforce each other. Even if defence functions solely as punishment without any direct effects on intrusion levels, cautiousness and aggressiveness will co-evolve to produce stable resource ownership with low theft.